

SHORT COMMUNICATION

Prey and predatory behavior of two zodariid species (Araneae, Zodariidae)

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Abstract. In this study, we investigated whether two plesiomorphic zodariid species, *Lachesana insensibilis* Jocqué 1991 and *Pax islamita* (Simon 1873), both from Israel, possess adaptations for myrmecophagy similar to those of apomorphic zodariid genera. Our analysis focused on the predatory behavior and potential prey of these two spider species. We deduced that *P. islamita* does not feed on ants in nature since these were not present in its microhabitat. In the habitat of *L. insensibilis*, however, ants were very abundant, and thus they may serve as an important diet component. In the laboratory, both species were able to subdue a wide variety of prey and therefore should be considered polyphagous. They used a conditional capture strategy. Safe prey was handled by grasping and holding it in a basket-like manner. Dangerous prey such as ants were attacked, released, and finally held in the chelicerae while the spider held its own legs at a safe distance. Both species were able to overcome ants if they were not larger than the spiders. We conclude that both species possess behavioral pre-adaptations for myrmecophagy.

Keywords: Specialization, adaptations, myrmecophagy, *Pax*, *Lachesana*

With more than 800 species, zodariid spiders represent one of the most diversified families of spiders (Platnick 2008). Yet the natural history of these spiders is very poorly known. Of all 74 genera known to date, only the genus *Zodarion* has been repeatedly investigated (e.g., Harkness 1976; Pekár & Král 2001). Information on the predatory behavior and prey is available for only eight genera of zodariid spiders: *Lachesana*, *Lutica*, *Habronestes*, *Psammoduon*, *Diores*, *Trygetus*, *Zodariellum*, and *Zodarion* (Allan et al. 1996; Jocqué & Dippenaar-Schomean 1992; Marikovskij & Tystshenko 1970; Ramirez 1995; Rössl & Henschel 1999; Pekár et al. 2005). The latter four genera belong to the Zodariinae, while the first four are considered plesiomorphic. These “primitive” zodariids appear to be polyphagous, while all genera within Zodariinae are presumably myrmecophagous or termitophagous (Jocqué 1991; Dippenaar-Schoeman & Jocqué 1997). *Zodarion* is apparently strictly myrmecophagous and is unable to subdue prey other than ants (Pekár 2004; Pekár & Toft, accepted).

Myrmecophagy has been observed in representatives of several different spider families beside Zodariidae, including Gnaphosidae, Salticidae, Theridiidae, and Thomisidae (e.g., Castanho & Oliveira 1997; Heller 1976; Jackson et al. 1998; Porter & Eastmond 1982). Ant-eating spiders, including *Zodarion*, use specialized prey capture behavior to overcome ants (Pekár 2004) and may possess morphological and metabolic adaptations as well (Pekár et al. 2008).

Our aim in this study was to investigate whether plesiomorphic representatives of Zodariidae feed on ants in nature and whether they possess adaptations for myrmecophagy. We examined the predatory behavior and trophic niche of two species that occur in Israel: *Lachesana insensibilis* Jocqué 1991 and *Pax islamita* (Simon 1873).

Individuals of *L. insensibilis* (body size 8–14 mm) were collected by hand in sand dunes near Mashabbim (Negev Desert, 31°0'5"N, 34°45'20"E). The burrows in the sand had no visible openings. The spiders were located by observing the search behavior of a spider-hunting wasp (*Pedipompilus* sp., Pompilidae). Once a burrow was located by the wasp, we dug the spider out of the sand using a trowel. Altogether, 33 individuals (3 males, 6 females, and 24 juveniles) were collected. Individuals of *P. islamita* (body size 4–9 mm) were collected in a Mediterranean forest close in the Adulam Nature Reserve (Bet Guvrin, 31°38'30"N, 34°56'4"E) by sifting the leaf litter through a sieve (60 × 40 cm, mesh size 7 mm) and by hand collecting. Juvenile

P. islamita spiders were found to hide in igloo-shaped retreats made of leaf litter particles, while sub-adult individuals rested in a crevice under stones. Altogether 59 juveniles (including sub-adults) and 2 females were collected. Identity of both species was determined using Levy (1990) and Jocqué (1991). Voucher specimens of both spider species are deposited in the collection of arachnids of the Department of Botany and Zoology, Masaryk University.

In each habitat, we investigated the potential prey of the two spider species by recording frequency of occurrence of invertebrates (> 2 mm) in the spiders' microhabitats. Our strategy for examining potential prey varied by location. In Adulam, we sifted through the leaf litter with a sieve, whereas in Mashabbim we searched the ground surface both during the day and night. All arthropods were collected and identified to order and/or family.

In the laboratory, we investigated capture success of the two spider species. Specimens of *P. islamita* were put singly in a Petri dish (diameter 6 cm). As *L. insensibilis* individuals were agitated when placed in the dish, the experiments were performed in glass containers (8 cm in diameter, 30 cm tall) filled with sand. Each spider was offered a variety of prey that either was endemic to the spider's natural environment or came from laboratory breeding cultures (Table 1). The interval between successive feedings was 10 days. Total body length of each offered prey was measured and its size was expressed as a ratio to the spider's total body length. In the case of *L. insensibilis*, nearly all prey was smaller than the spiders. Each trial with prey lasted 5 min. At the end of the trial, we assessed the prey according to whether it was attacked and consumed or untouched. The trials were recorded on video (using CANON MVX-350i camera) and the recorded predatory behavior was then analyzed.

The potential prey of *L. insensibilis* (Fig. 1) included Coleoptera imagoes (Tenebrionidae – 31%, Curculionidae – 15%, Carabidae – 5%) (altogether 51%, $n = 264$), followed by Formicidae (33%). The potential prey of *P. islamita* (Fig. 2) was comprised of Isopoda (34%, $n = 278$), Araneae (26%), and Collembola (18%). Ants were not recorded in the microhabitat.

In the laboratory, juveniles and females of *L. insensibilis* captured (i.e., attacked and consumed) various prey, mainly flies, ants and beetles (Table 1), but also crickets, spiders, termites and cockroaches. These spiders ignored true bugs and caterpillars. Males of *L.*

Table 1.—Percentage (*n*) of successful capture (i.e., attack followed by consumption) of various prey taxa in the laboratory by two zodariid species.

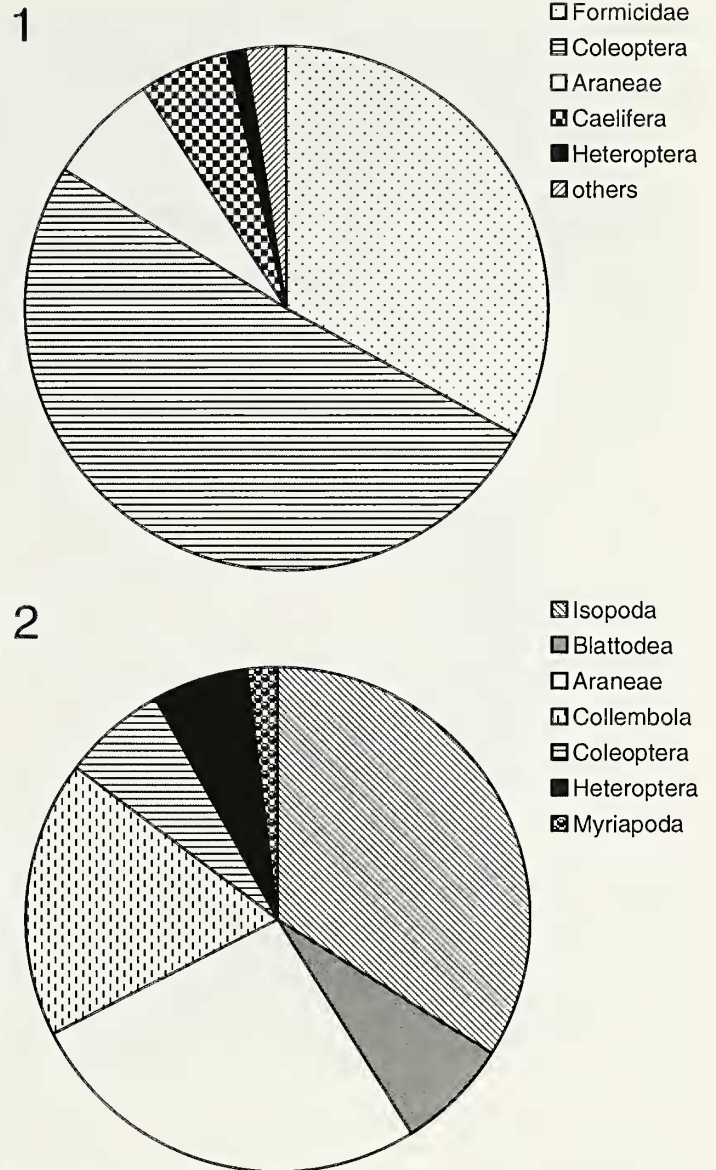
Prey type	Prey size [mm]	Zodariid species	
		<i>Lachesana insensibilis</i>	<i>Pax islamita</i>
Araneae (<i>Harpactea</i> sp.)	5–8	44 (19)	43 (21)
Isopoda	6–10	–	0 (10)
Collembola	2–3	–	50 (10)
Zygentoma	8–12	–	90 (10)
Blattodea	5–9	48 (21)	63 (16)
Isoptera	7–9	64 (22)	87 (30)
Ensifera (<i>Acheta domestica</i>)	6–9	65 (23)	57 (21)
Heteroptera	8–10	0 (15)	–
Coleoptera larvae (<i>Tenebrio molitor</i>)	20–25	100 (10)	70 (15)
Coleoptera imagoes (<i>T. molitor</i>)	13–15	80 (10)	–
Diptera (<i>Drosophila hydei</i>)	3–4	100 (21)	71 (14)
Lepidoptera (caterpillars)	15–20	0 (15)	–
Formicidae (<i>Messor</i> sp.)	7–12	85 (20)	53 (17)

insensibilis refused to attack any prey after molting to adult stage. It is well known that males of many spider species cease prey capture after reaching adulthood (e.g., Givens 1978). Adult males of *L. insensibilis* possess uniquely curved fangs (Levy 1990) that might handicap them in prey capture. Individuals of *P. islamita* captured mainly Isoptera, Coleoptera (larvae), Diptera, and Blattodea. They attacked woodlice but did not consume them. Ants were subdued only if they were small (less than the spider's body length).

Lachesana insensibilis individuals attacked prey either from inside the silk-lined burrow or on the sand surface within close proximity of the covered entrance. The prey was subsequently pulled inside. The burrow was narrow and long (up to 25 cm), with the top plugged with a collar made of sand. The remnants of the prey were stored in the bottom of the burrow.

Both spider species exhibited similar capture behavior that differed according to the size and safety of the prey. Springtails, cockroaches, crickets, flies, isopods, bristletails, and true bugs were grabbed by the forelegs and held in a basket-like manner using the first three pairs of legs. The bite was usually administered to the dorsal side of the thorax or abdomen and the prey, such as a cockroach, was held until completely immobilized (Fig. 3). *Tenebrio* larvae were grabbed by the forelegs and bitten on the head or at the distal end of body. Typically, the spider tried to hold on to the larvae, but if the larva struggled extensively, the spider released it (Fig. 4). Once immobilized, the larva was grabbed by its head and held in a basket-like manner. Ants, spiders, and termites were grasped and bitten on the dorsal side of the head/prosoma, and then released. After several minutes, the still-trembling prey, such as a termite, was grabbed and bitten firmly on the dorsal side of the thorax such that the termite head (and mandibles) was oriented away from the spider. The prey was never held in a basket-like manner. Based on these results, certain prey (springtails, beetles, cockroaches, crickets, flies, isopods, bristletails, true bugs) were classified as "safe" while others were classified as "dangerous" (ants, spiders, termites). *Pax islamita* was significantly more successful in capturing safe prey than dangerous prey (logistic regression, GLM – binomial errors, $\chi^2_1 = 11$, $P = 0.001$). The spiders had a 50% chance of capturing safe prey 3 times larger than their body, while for dangerous prey it was only 1.5 times larger (Fig. 5).

Results of this study show that neither *L. insensibilis* nor *P. islamita* is an ant-eating stenophagous predator. In fact, laboratory experiments suggest that both species are polyphagous. Combining the results of potential prey with data on capture success, we deduced that *P. islamita* feeds naturally on cockroaches, insect larvae, and other spiders and probably does not feed on ants at all. *Lachesana*



Figures 1, 2.—Proportion of potential prey found in microhabitats of the two study species. 1. *Lachesana insensibilis* ($n = 264$). 2. *Pax islamita* ($n = 278$).

insensibilis, however, appears to feed on ants and beetles in the field. Due to its larger body size, *L. insensibilis* has better chances of subduing ants than *P. islamita*.

Our results are in agreement with observations of *Lachesana tarabaevi* Zonstein & Ovtchinnikov 1999 from Central Asia. Individuals of this species live in similar narrow burrows and emerge at twilight to hunt at night on the surface within close proximity of their burrows. Analysis of prey remains showed that this species preys mainly on harvester ants (*Messor* sp.) and on woodlice (Zonstein & Ovtchinnikov 1999). Although we have not seen *L. insensibilis* hunt on the surface either during the day or at night, we assume it is nocturnal. We doubt that *L. insensibilis* would feed on woodlice as these do not occur on sand, but *Messor* ants were common in the habitat.

American species of the genus *Lutica* that are very closely related to *Lachesana* show similar predatory behavior. They are also fossorial, building silk-lined tunnels in sand just below the surface in the coastal sand dunes. They catch prey either from inside the burrow by hanging on the ceiling upside down and lunging through the wall or on the surface (Gertsch 1979). In the laboratory, they accepted fruit flies,



Figures 3, 4.—*Pax islamita*. 4. Handling a safe and small prey (cockroach). 5. Handling a safe but large prey (*Tenebrio* larva). Photos: S. Henriques.

houseflies, and beetle larvae but in the field they were found to feed primarily on wireworm larvae, the most abundant insects on dunes (Ramirez 1995).

Another plesiomorphic species, *Psammoduon deserticola* (Simon 1910), from the Namib Desert, attacked tenebrionid larvae on the sand's surface. In the laboratory, this spider preferred to catch tenebrionid larvae over fly larvae and *Thysanura*. It may feed on ants and termites as well (Rössl & Henschel 1999).

Lachesana insensibilis and *P. islamita* showed conditional capture strategy. The capture behavior of safe prey was similar to that observed in lycosids that constrain struggling prey with stout legs (Rovner 1980). Both zodariid species also possess stout legs and used them to hold all other prey in a basket-like manner. Dangerous prey, namely ants, were in turn captured using a bite-and-release tactic, similar to that of ant-eating spiders. Both *L. insensibilis* and *P. islamita* grabbed hold of an incompletely immobilized ant so the capture success depended on the relative size of the prey. Ant-eating *Zodarion* spiders deliver a bite usually to the ant's leg and wait until the ant is completely immobilized; thus, these spiders are able to overcome ants much larger than themselves (Pekár 2004). Neither *L. insensibilis* nor *P. islamita* seem to possess any morphological adaptations for myrmecophagy. It remains to be investigated whether

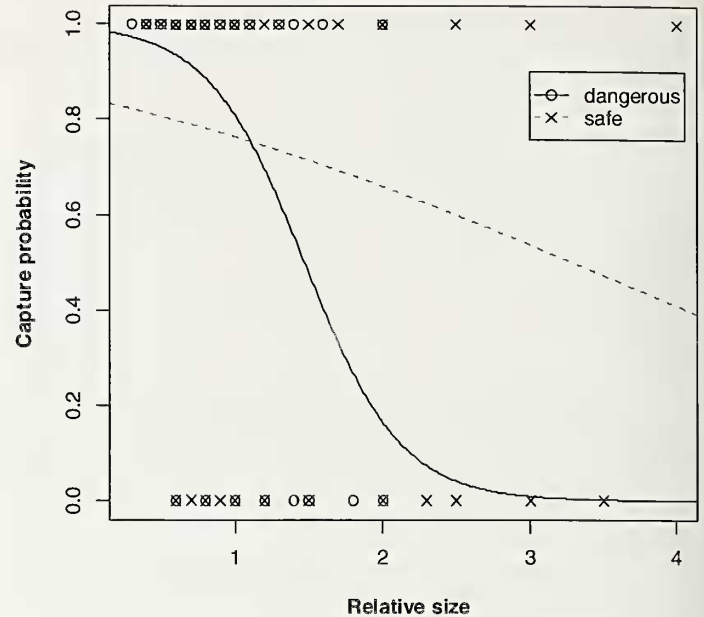


Figure 5.—Probability models for capture of dangerous and safe prey by *P. islamita*. Relative size represents the ratio of the prey body length to the spider body length.

L. insensibilis and *P. islamita* are metabolically adapted to consuming ants. *Zodarion*, for example, is adapted to such an extent that alternative prey (e.g., flies) do not provide them with the required nutrition (Pekár & Toft, accepted).

We conclude that unlike many dysderid, clubionid, lycosid, gnaphosid, salticid, or corinnid spiders that avoid ants (Bristowe 1939), "primitive" zodariid spiders possess behavioral pre-adaptations that enable them to handle ants. Yet these adaptations allow them to catch only small ants.

We would like to thank S. Henriques and M. Řezáč for help with collecting and L. Sentenská and E. Lízarová for help with rearing the spiders. We also thank the Israel Nature and National Parks authority for permission to collect in Adulam Reserve. The study was supported by the E.U. Specific Support Action program provided by the Jacob Blaustein Center for Scientific Cooperation given to SP and by the grant no. 206/06/0629 of the Czech Science Foundation. This is publication no. 625 of the Mitrani Department of Desert Ecology.

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Manuscript received 3 June 2008, revised 25 September 2008.